Z. Säugetierkunde **63** (1998) 137–146

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Variation and secondary sexual dimorphism of skeletal characters in *Glossophaga morenoi* and *G. leachii* from southwestern México (Chiroptera: Phyllostomidae)

By Celia López-González and O. J. Polaco

Department of Biological Sciences, Texas Tech University, Lubbock, Texas, USA and Laboratorio de Paleozoología, Subdirección de Laboratorios y Apoyo Académico, Instituto Nacional de Antropología e Historia, México

Receipt of Ms. 17. 12. 1996
Acceptance of Ms. 06. 10. 1997

Abstract

Morphometric variation and secondary sexual dimorphism were evaluated and compared in 9 cranial and 23 postcranial characters of *Glossophaga leachii* and *G. morenoi*. Analysis of coefficients of variation (CV) showed that the degree of variation as well as its pattern are very similar for both species, with their CVs being lower than those found in birds and other mammals. Sexual dimorphism was tested using ANOVA and MANOVA. Results were significant for three cranial and three postcranial characters of *G. leachii*, as well as for nine postcranial traits of *G. morenoi*. Results of MANOVA on the same characters confirmed univariate results. Females are larger than males in most variables for both species, presumably as a result of higher energetic and physical demands of pregnant females and nursing mothers. Importance values in discriminating between sexes were calculated for each variable, importance profiles constructed, and significance of their correlations tested for cranial and postcranial characters separately to reassess the hypothesis that once differentiation occurs at the specific level, sexual dimorphism is no longer constrained in the same fashion as in the ancestral condition. Our results suggest that for cranial characters that is the case. For postcranial elements, however, importance profiles are highly correlated, suggesting that for characters with presumably higher fitness value, ancestral constraints remain after speciation has occurred.

Key words: *Glossophaga leachii*, *G. morenoi*, Dimorphism, morphometrics, skeleton

Introduction

Sexual dimorphism has been a matter of interest to biologists at least as far back as Darwin (1859). The mechanisms by which secondary sexual differences arise and are maintained within a population have been studied from the point of view of geneticists (Arnold 1985; Lande 1987), ecologists (Shine 1989), and systematists (Mayr 1942) alike. There has been an ongoing and yet unresolved controversy regarding which characters are selected to produce the dimorphic condition, and a number of hypotheses have been proposed (Selander 1966; Ralls 1976; Myers 1978; Shine 1989). Nevertheless, there seems to be consensus on the idea that maintenance of dimorphism is due, at least in part, to differential regulation of gene expression in males and females, and that it should be constrained within species inasmuch as genes are coadapted and characters involved are the product of pleiotropism (Lande 1987).

Consistent with this is the idea that populations within a species very likely would express sexual dimorphism via a consistent suit of morphometric characters because the

groups are linked to the degree to which they share gene pools (Willig and Hollander 1995). It is also possible, as these authors state, that although there may exist different balances among forces shaping dimorphism in each population, certain characteristics are more likely to change whereas others are more phylogenetically constrained. They also hypothesize that once speciation has occurred, coadapted gene complexes and genetic dynamics in general no longer constrain the expression of dimorphism, and that for the most part, patterns of intersexual variation are species-specific and relatively unrelated to systematic arrangements beyond the specific level.

Nectar-feeding bats of the genus *Glossophaga* are common in lowlands of Neotropical America (Webster 1993). Recently, large samples of *Glossophaga morenoi* and *G. leachii* were collected in southwestern México. Variation in *Glossophaga*, including sexual dimorphism, has been studied by Webster (1993), but his work was restricted to skull and external forearm and digit characters. This has been the case in most analyses of morphometric variation in bats (e.g. Power and Tamsitt 1973; McLellan 1984; Bogdanowicz 1992; Gannon et al. 1992), because mammals are traditionally kept as dried skins and skulls or the complete specimen is fixed in alcohol. From our samples, however, complete skeletons of all the specimens were available, allowing for the study and comparison of cranial and postcranial characters within each population. Species of the genus *Glossophaga* have gene pools that, although independent from each other, share a close common phylogenetic history. Similar patterns of sexual dimorphism are expected from them, with differences arising from differential selective pressures or distinct genome combinations inherited from their ancestral, common gene pool. Because both of the populations studied here were sampled in the same habitat type, variation due to ecological factors shaping particular characteristics of these organisms is assumed to be relatively constant.

The purpose of our study is to describe and compare the degree of intrapopulational variation within a sample of *G. leachii* and *G. morenoi*, with emphasis on secondary sexual dimorphism. We describe such differences from an univariate as well as a multivariate perspective, following the assertion of Willig et al. (1987) that, when analyzing large morphometric data sets in which characters are correlated, overall group differences are better evaluated by using multivariate techniques. Using the methodology developed by Willig and Hollander (1995), we assess the importance of particular characters in determining sexual dimorphism, and compare the expression of sexual differences between cranial and postcranial characters. Additionally, we reassess Willig and Hollander's (1995) hypothesis of relatively independent patterns of intersexual variation beyond the level of species.

Material and methods

Specimens were collected in two road culverts in southwestern México, 33 specimens of *G. leachii* in Oaxaca state (7 km N, 10 km E Tapanatepec, 730 m), and 40 of *G. morenoi* in Michoacán (22.2 km N, 7.0 km W Infiernillo, 350 m). Bats were caught in similar habitats, a scrub thorn-forest of *Prosopis* spp. and *Acacia* spp. (Rzedowski 1988). Four additional specimens of *G. morenoi*, collected about one kilometer apart from the culvert at Infiernillo, were also included in the latter sample. All specimens are adult (phalangeal epiphyses completely fused and cranial sutures well ossified), and were prepared as standard museum skeletons. Specimens are deposited in the osteological collection of the Subdirección de Laboratorios y Apoyo Académico (DP), Instituto Nacional de Antropología e Historia, México, D.F., México (*G. morenoi*: DP 6019–6021, 6817–6851; *G. leachii* DP 6465–6483).

A total of 9 cranial variables was measured following Webster (1993). Twenty-three postcranial characters were taken following López-González (1992). Measurements were taken to the nearest 0.1 mm using a digital caliper. All variables are greatest (maximum) lengths or widths. Their acronyms are as follow: length of the skull (GLS), condylobasal length (CBL), mastoid breadth (MAW), zygomatic breadth (ZYG), interorbital width (INT), length of maxillary toothrow (MAX), width across molars (WAM), depth of braincase (SKD), length of mandibular toothrow (MAN), length of first metacar-

pal (MCI), length of second metacarpal (MCII), length of third metacarpal (MCIII), length of fourth metacarpal (MCIV), length of fifth metacarpal (MCV), length of first phalanx of digit I (PlI), length of first phalanx of digit III (PlIII), length of second phalanx of digit III (P2III), length of first phalanx of digit IV (PlIV) length of first phalanx of digit V (P1V), length of radius (GLRA), length of humerus (GLHU), width of proximal epiphysis of humerus (GWPH), width of distal epiphysis of humerus (GWDH), length of the scapula (GLSC), width of the scapula (GWSC), height of atlas (GHAT), width of atlas (GWAT), length of innominate bone (GLPE), internal length of foramen obturatum (FORA), length of femur (GLFE), length of tibia (GLTI), length of fibula (GLFI).

To describe and compare the variation for each character within populations, coefficients of variation (CV) were determined for all of the variables in each population. In further analyses, measurements were transformed to their natural logarithms. Missing values were calculated by regressing each variable against the greatest length of the radius and substituting the estimated values for the missing ones. Secondary sexual dimorphism was tested for each character within each species using univariate analyses of variance (ANOVA). Multivariate differences between sexes were tested using MANOVA. Step-wise discriminant function analyses were performed to obtain linear combinations of variables that best described the differences between groups (sexes). Importance values (I) for each variable were calculated using the formula given by Willig and Hollander (1995). Because this is a two-group analysis, the formula is simplified to the square of the Pearson's correlation between the discriminant-function score and the original value of each character for each individual. Results are expressed in bar diagrams (importance profiles), in which the height of the bar for a particular character is equal to its importance value. The degree of concordance between character suites, in terms of importance profiles of variables, was evaluated by calculating the Pearson's correlation of importance values for each character between groups. To allow for comparison, all tests were performed on cranial and postcranial characters separately. Analyses were conducted using the Statistical Analysis System (SAS Institute Inc. 1987).

Results and discussion

General variation

Coefficients of variation are very similar for the two species analyzed (Tab. 1). In both of them, the greatest length of the skull (GLS) showed the lowest CV, whereas the depth of braincase (SKD) in *G. leachii*, and the greatest width across molars (WAM) in *G. morenoi*, showed the highest. CV values for skull characters are near those reported by Webster (1993) for all the species of *Glossophaga.* He reports CVs less than 3.5 for most of the measurements. CVs for postcranial measurements of *Glossophaga morenoi* range from 2.31 for the greatest height of atlas (GHAT), to 6.51 for the greatest length of the fibula (GLFI) (Tab. 1). *G. leachii* presents a similar range of CVs, with the lower limit (2.11) given by the greatest width of the distal epiphysis of humerus (GWDH) and the upper one (7.95) by the internal length of the foramen obturatum (FORA). In both species, CVs of postcranial measurements fall slightly below the typical values found in mammals (Bader and Hall 1960) and are closer to those found in birds, organisms considered by these authors as much less variable than mammals.

For both species, when wing elements are considered in proximo-distal series, CVs progressively increase the more distally they are positioned (Tab. 2). Bader and Hall (1960) obtained similar results in *Myotis* for digits completely embedded in the flight membrane, and a random distribution of CVs for bones of digit I. They explained the increase in CV as a result of a progressive replacement of bone by unossified connective tissue, and considered this trend to be in direct association with the time of onset of osteogenesis. However, *G. morenoi* and *G. leachii* showed the same pattern also in digit I, which is not in close association with the flight membrane. Additionally, it has been observed in *G. morenoi* (López-González 1992) that elements of digit I complete fusion and ossification right after birth (enabling the immediate use of the thumbs by newborns for clinging to the mother), whereas the process is completed almost at adulthood for the

Table 1. Mean, standard deviation, and coefficient of variation for 32 skeletal variables of *G. leachii* (18 males, 15 females) and *G. morenoi* (24 males, 20 females). Upper row, males; lower row, females. Coefficients of variation are shown for both sexes together.

	G. leachii			*G. morenoi*		
CHAR.	MEAN	STD	CV	MEAN	STD	CV
Cranial						
GLS	20.65	0.33	1.57	21.25	0.31	1.64
	20.91	0.26		21.42	0.38	
CBL	19.25	0.35	1.71	20.25	0.32	1.82
	19.55	0.21		20.44	0.40	
MAW	9.18	0.20	2.08	8.74	0.18	1.86
	9.13	0.18		8.78	0.13	
ZYG	9.59	0.17	1.91	9.21	0.23	2.46
	9.52	0.19		9.18	0.21	
INT	4.51	0.11	2.22	4.56	0.13	2.67
	4.57	0.07		4.57	0.10	
MAX	6.96	0.21	2.96	7.31	0.14	2.39
	7.13	0.16		7.41	0.22	
WAM	5.59	0.13	2.38	5.60	0.14	2.94
	5.63	0.13		5.61	0.19	
SKD	7.34	0.18	3.41	6.97	0.15	2.44
	7.23	0.30		6.89	0.19	
MAN	7.37	0.18	2.37	7.76	0.14	2.35
	7.47	0.16		7.81	0.22	
Postcranial						
MCI	3.26	0.18	5.82	3.13	0.17	4.82
	3.32	0.19		3.16	0.13	
MCII	30.35	0.97	3.49	27.71	1.01	4.39
	30.91	1.13		28.12	1.35	
MCIII	35.63	0.85	2.81	33.06	0.99	3.33
	36.19	1.12		33.09	1.09	
MCIV	32.61	0.82	2.85	30.14	0.87	3.37
	32.95	1.05		30.80	1.01	
MCV	30.65	0.71	2.93	29.08	0.93	3.38
	31.37	0.97		29.82	0.88	
P1I	4.17	0.28	5.87	4.22	0.24	6.22
	4.26	0.19		4.35	0.27	
P1III	12.35	0.44	3.73	12.43	0.52	3.59
	12.53	0.49		12.51	0.36	
P2III	17.01	0.63	3.47	15.11	0.70	3.95
	16.91	0.54		15.24	0.42	
P1IV	9.97	0.34	3.53	9.64	0.32	3.36
	9.92	0.37		9.82	0.32	
P1V	8.71	0.37	4.96	8.68	0.32	3.29
	8.76	0.50		8.73	0.24	
GLRA	34.95	0.99	3.04	32.69	0.86	2.87
	35.63	1.07		33.25	0.90	
GLHU	21.62	0.56	2.99	20.33	0.51	2.57
	22.24	0.60		20.83	0.40	
GWPH	3.92	0.11	3.40	3.46	0.11	3.19
	3.96	0.16		3.51	0.11	
GWDH	3.79	0.08	2.11	3.55	0.08	2.41
	3.81	0.09		3.57	0.09	
GLSC	14.67	0.35	2.47	12.61	0.31	2.68
	14.75	0.38		12.65	0.23	

Table 1. (Continued)

	G. leachii			*G. morenoi*		
CHAR.	MEAN	STD	CV	MEAN	STD	CV
GWSC	6.35	0.18	2.76	5.67	0.17	2.85
	6.38	0.18		5.72	0.12	
GHAT	3.32	0.11	2.90	3.07	0.07	2.31
	3.35	0.07		3.04	0.06	
GWAT	6.12	0.19	3.06	5.76	0.18	3.25
	6.14	0.19		5.89	0.16	
GLPE	9.53	0.19	3.94	8.70	0.22	3.51
	10.10	0.32		9.06	0.22	
FORA	2.19	0.16	7.95	2.10	0.11	5.79
	2.27	0.19		2.15	0.14	
GLFE	13.42	0.42	3.01	12.61	0.36	3.48
	13.53	0.39		12.83	0.38	
GLTI	12.75	0.42	3.66	11.67	0.30	3.50
	12.95	0.51		11.98	0.37	
GLFI	8.44	0.50	5.90	7.89	0.53	6.51
	8.54	0.51		8.26	0.45	

Table 2. Coefficients of variation of the forelimb elements of *G. leachii* (upper rows) and *G. morenoi* (lower rows) arranged in proximo-distal series. More proximal elements to the left, more distal ones to the right. Second phalanges of digits IV and V were not considered.

GLHU	GLRA	MCI	P1I		Digit
2.99	3.04	5.82	5.86		I
2.57	2.87	4.82	6.22		
		MCII			
		3.49			II
		4.39			
		MCIII	P1III	P2III	
		2.81	3.73	3.47	III
		3.33	3.59	3.94	
		MCIV	P1IV		
		2.84	3.53		IV
		3.37	3.36		
		MCV	P1V		
		2.93	4.95		V
		3.38	3.29		

rest of the wing elements. Alternative explanations are yet to be investigated for this trend, which also has been observed in forelimbs and hindlimbs of birds (Bader and Hall 1960).

Coefficients of variation for the length of the femur and tibia (Tab. 1) are higher than those for humerus and radius in both species. Elements of the first digit of manus, those not directly associated to the flying membrane, show higher CVs than the homologous elements of the other digits, modified for flight. It is possible to speculate on the importance for survival of keeping a narrow span of variation in structures involved with lift and loading in a flying animal compared to other elements of the same organism; one would expect the former to be the more conservative, and therefore to show lower CVs. Such a trend, however, is not clear within species for the skeletal structures studied.

Sexual dimorphism

ANOVA was significant for three cranial variables in *G. leachii*. Coinciding with the univariate analyses, the result of the MANOVA was also significant (Tab. 3). In contrast, none of the cranial variables analyzed was significantly dimorphic for *G. morenoi*, and multivariate results were also nonsignificant. Importance profiles are different for each species (Fig. 1), which supports the idea that there is a species-specific pattern in the expression of sexual differences, as suggested by the results of ANOVA and MANOVA. This is further indicated by a nonsignificant correlation between importance profiles ($r = 0.6177$, $P = 0.0763$).

Results of postcranial comparisons, however, differ considerably from the cranial results. Nine variables were significantly dimorphic in *G. morenoi*, whereas only three were

Table 3. F-values and associated probabilities of ANOVA and MANOVA for sexual differences in 32 skeletal characters of *G. leachii* and *G. morenoi*. Asterisks indicate significance at $\alpha = 0.05$.

	G. leachii (N = 33)		*G. morenoi* (N = 44)	
VAR	F	P	F	P
Cranial				
GLS	5.71	0.023*	2.23	0.142
CBL	8.38	0.07*	1.93	0.172
MAW	0.41	0.528	0.64	0.429
ZYG	0.46	0.504	0.07	0.792
INT	3.04	0.091	0.09	0.760
MAX	6.44	0.016*	2.93	0.094
WAM	0.94	0.339	0.02	0.888
SKD	1.95	0.173	2.68	0.109
MAN	2.89	0.099	0.57	0.455
MANOVA	2.37	0.046*	0.87	0.555
Postcranial				
MCI	0.76	0.390	0.44	0.510
MCII	2.36	0.134	1.25	0.269
MCIII	2.61	0.116	7.07	0.011*
MCIV	1.03	0.318	5.25	0.027*
MCV	5.89	0.021*	7.09	0.011*
P1I	1.30	0.262	3.34	0.075
P1III	1.24	0.275	0.58	0.452
P2III	0.44	0.511	0.97	0.329
P1IV	0.21	0.647	3.36	0.074
P1V	0.08	0.780	0.38	0.541
GLRA	3.51	0.070	4.74	0.035*
GLHU	9.19	0.005*	11.98	0.001*
GWPH	0.43	0.515	1.99	0.166
GWDH	0.47	0.500	0.87	0.356
GLSC	0.39	0.539	0.23	0.636
GWSC	0.18	0.678	1.47	0.232
GHAT	0.66	0.423	1.17	0.285
GWAT	0.06	0.812	6.05	0.018*
GLPE	23.90	0.0001*	26.78	0.0001*
FORA	1.66	0.207	1.37	0.249
GLFE	0.57	0.456	3.89	0.055
GLTI	1.45	0.237	9.17	0.004*
GLFI	0.35	0.556	6.26	0.016*
MANOVA	1.59	0.238	2.36	0.028*

so for *G. leachii.* Results of MANOVA are in agreement with the univariate analyses, multivariate differences are not significant for *G. leachii* and significant for *G. morenoi.* Unlike in the skull, importance profiles of postcranial characters are highly correlated ($r = 0.847$, $P = 0.0001$). This is graphically evident also. Although importance values are different for each species, the patterns of the profiles are very similar (Fig. 1).

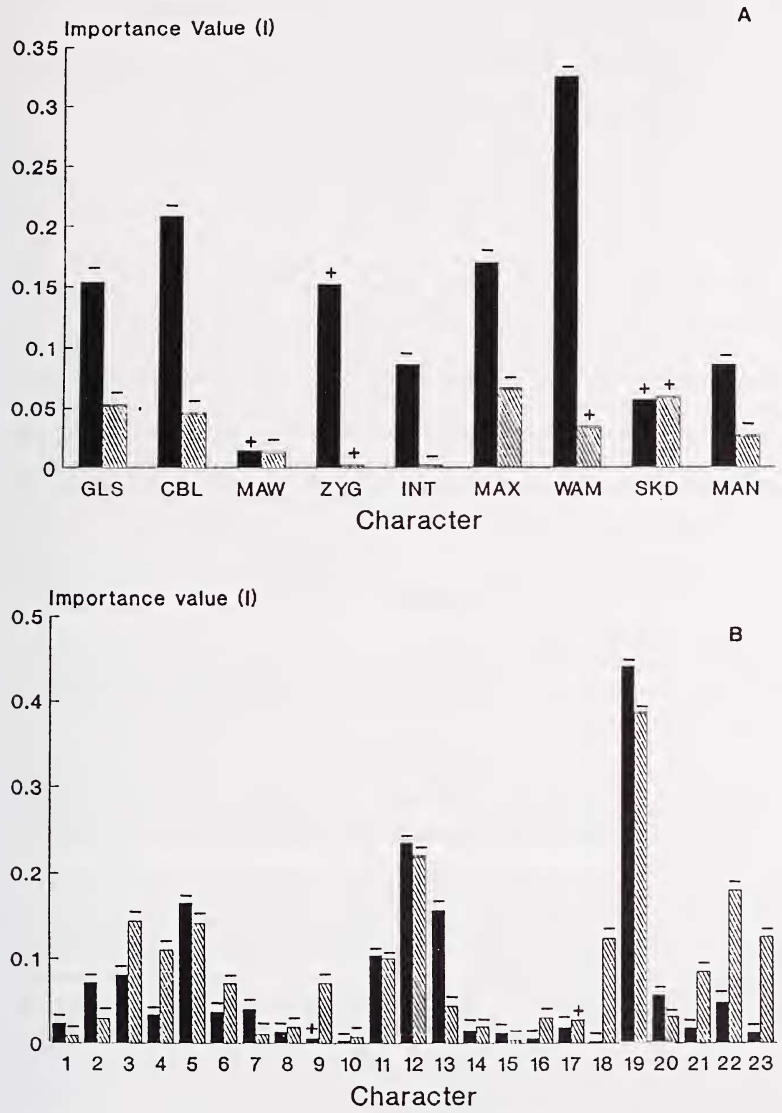

Fig. 1. Importance profiles for cranial (A) and postcranial (B) characters for *Glossophaga leachii* (black bars) and *G. morenoi* (hatched bars). Height of a bar for a given character estimates its relative importance in distinguishing between sexes. Females larger than males are indicated by a minus (–) on top of bar, males larger than females by a plus (+). Numbers in diagram B correspond to variables as follows: 1 = MCI , 2 = MCII, 3 = MCIII, 4 = MCIV, 5 = MCV, 6 = P1I, 7 = P1III, 8 = P2III, 9 = P1IV, 10 = P1V, 11 = GLRA, 12 = GLHU, 13 = GWPH, 14 = GWDH, 15 = GLSC, 16 = GWSC, 17 = GHAT, 18 = GWAT, 19 = GLPE, 20 = FORA, 21 = GLFE, 22 = GLTI, 23 = GLFI.

The variable with the higher importance value in both species is the length of the innominate bone. This is the skeletal structure where sexual dimorphism is most visually apparent in many mammals. In males of *Glossophaga*, the posteriormost part of the pubic bone bends medially to form a symphysis pubis. In females, it is directed backwards, resulting in a longer pelvis. The rest of elements that better describe sexual differences (those with the highest importance values) are directly involved with flight (MCIII, MCIV, MCV, GLRA, and GLHU) or with roosting (GLTI, GLFI) (Fig. 1).

Several hypotheses have been proposed to explain the origin and maintenance of sexual dimorphism. Competition among individuals of one sex, usually males, has been proposed as a selection process acting on morphological and behavioral traits (Trivers 1972). It has also been suggested that size differences between sexes may reduce competition for resources (Selander 1966). Myers' (1978) study on sexual dimorphism in vespertilionid bats showed that the degree of difference between males and females is greater for those species with greater fetal or neonatal weight, and that wing size of females is larger than that of males of comparable body size. He concluded that sexual dimorphism in those bats is influenced by demands of large fetuses. However, Williams and Findley (1979) considered that larger sizes of vespertilionid females are due to increased demands of energy during pregnancy, although they do not deny that weight loading may also be important. Ralls' (1976) hypothesis of the "big mother" proposes that a larger female would produce a larger baby with greater chances of survival because she could provide more or better milk, and could be better at carrying or defending her young.

Our data from the postcranial skeleton do not yield useful information to evaluate dimorphism as a result of sexual selection or competition for resources. They are, however, consistent with Myers' (1978) interpretation. Females are larger than males in those characters with high importance values, which are also associated with structures specifically involved in flying and roosting, rather than with general size. Considered as a whole, sexual differences found in the skeleton do not contradict Ralls' (1976) hypothesis either, and it is possible that being a "better mother" in these species has to do with her ability to carry and nourish large fetuses and young.

Regardless of the selective forces involved in maintaining these differences, our results also suggest that the skull, as a structure, is less constrained to change than the postcranial skeleton is. Willig and Hollander (1995) compared two populations of *G. soricina* from Brazilian caatinga and cerrado using cranial characters comparable to those of this study. Although they found significant differences between sexes in both sites, profiles of importance were not significantly correlated. Samples of *G. commissarisi* comparable to ours were analyzed by Webster (1993); he reported nonsignificant sexual differences for the variables measured.

Willig and Hollander (1995) hypothesized that legacy of gene pools in the past should limit the degree to which differences between sexes can be expressed in dimorphic taxa, and that correlations of profiles of importance values should decrease as comparisons are made at increasingly higher taxonomic levels. Using cranial characters, they found that most of their data did not correspond to this expectation. Thus, they concluded that once differentiation at the specific level occurs, expression of dimorphism is no longer constrained in the same way. Our cranial data are consistent with this conclusion, with the two species of *Glossophaga* differing in their expression of sexual dimorphism. They also differ with respect to the populations of *G. soricina* analyzed by Willig and Hollander (1995), and from those of *G. commissarisi* studied by Webster (1993).

In contrast, postcranial profiles show a high degree of coincidence. Even though for some characters sexes are not significantly different in *G. leachii* at the alpha level selected for this study (0.05), results suggest that sexual differences are expressed in a similar manner for this species and for *G. morenoi*. The postcranial profiles indicate that at least for these two species, the constraints to the expression of dimorphism from their

common ancestor remained in both taxa. Either there is a common selective force that keeps the patterns of variation between sexes constant, or speciation has taken place so recently that not enough time for significant changes has yet elapsed. The latter is more difficult to reconcile with what is observed in the skull, in which, apparently, differences between sexes are changing independently. A stronger selective constraint for each sex, at least in wing and hindlimb proportions, seems to be more likely, whereas for the skull, more plasticity is allowed. Patterns of intersexual variation may persist if the same selective pressures remain acting over the daughter species. Other characteristics, less constrained, will experience changes along their independent, new evolutionary pathways. This is consistent with our present knowledge of the genus *Glossophaga.* Although the characters that define the genus have been consistently understood and applied by most taxonomists, taxonomy within the genus has been rearranged several times during this century, mostly because of the high variability and overlapping of those skull characters used to distinguish among species (Webster and Jones 1980; Polaco and Muñiz-Martínez 1987).

Morphological variation is a reflection of the evolutionary factors that shape phenotypes. When comparing the two species studied, the general patterns of variation in terms of CV's are essentially the same for both of them. When patterns of sexual dimorphism are considered, our results suggest that the skull, as a structure, has been less constrained to change than the postcranial skeleton has. Apparently, after speciation occurred, selective pressures affected the studied populations differently, so that some parts of individuals have been more liable to change than others. Regardless of the selective force involved in maintaining secondary sexual differences, importance profiles for postcranial characters indicate that, at least for these two species, the constraints to the expression of dimorphism from their common ancestor remained in both taxa.

Acknowledgements

We thank J. Juste B., R. D. Owen, and R. D. Stevens for their helpful comments to early versions of the manuscript. Robert Huber kindly translated the abstract.

Zusammenfassung

Unterschiede und sekundärer Sexualdimorphismus von Skeletmerkmalen bei Glossophaga morenoi und G. leachii des südwestlichen Mexiko (Chiroptera: Phyllostomidae)

Morphometrische Variabilität und sekundärer Sexualdimorphismus wurden in 9 cranialen und 23 postcranialen Merkmalen bei *Glossophaga leachii* und *G. morenoi* vergleichend untersucht. Eine Analyse der Variationskoeffizienten (VK) zeigte, daß das Ausmaß der Variation sowie dessen Struktur bei beiden Arten ähnlich war, mit einem geringeren VK als bei Vögeln und anderen Säugetieren. Sexualdimorphismus wurde mittels ANOVA und MANOVA untersucht. Drei craniale und drei postcraniale Merkmale zeigten sich signifikant bei *G. leachii* und neun postcraniale Charaktere bei *G. morenoi.* Eine MANOVA an diesen Merkmalen bestätigte die univariaten Ergebnisse. Bei beiden Arten waren die weiblichen Tiere in den meisten Variablen größer, wahrscheinlich adaptiv aufgrund höherer energetischer und physikalischer Anforderungen trächtiger Weibchen und säugender Mütter. Zur Trennung der Geschlechter wurden für jede Variable Gewichtungswerte berechnet. Gewichtungsprofile wurden daraus erstellt und die Signifikanz der Korrelationen zu cranialen and postcranialen Merkmalen separat getestet. Mit dieser Analyse wurde die Hypothese geprüft, daß bei einem bestimmten Differenzierungsgrad Sexualdimorphismus nich mehr in gleicher Weise bedingt wird wie in der evolutionär ursprünglichen Form. Unsere Daten legten nahe, daß dies bei Schädelmaßen in der Tat zutrifft. Bei postcranialen Merkmalen korrelieren die Gewichtungsprofile jedoch hoch signifikant, was darauf hindeutet, daß bei Merkmalen mit erwartet höherem Fitnesswert evolutionäre Zwänge nach erfolgter Arttrennung weiterbestehen.

Literature

Arnold, S. J. (1985): Quantitative genetic models of natural selection. Experientia **41**, 1296–1310.

Bader, R. S.; Hall, J. S. (1960): Osteometric variation and function in bats. Evolution **14**, 8–17.

Bogdanowicz, W. (1992): Sexual dimorphism in size of the skull in European *Myotis daubentoni* (Mammalia: Chiroptera). In: Prague studies in Mammalogy. Ed. by I. Horácek and V. Vohralík. Praha: Charles Univ. Press. Pp. 17–25.

Darwin, C. R. (1859): On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for life. London: John Murray.

Gannon, M. R.; Willig, M. R.; Jones, J. K., Jr. (1992): Morphometric variation, measurement error, and fluctuating asymmetry in the red fig-eating bat (*Stenoderma rufum*). Texas J. Sci. **44**, 389–404.

Lande, R. (1987): Genetic correlations between the sexes and the evolution of sexual dimorphism and mating preferences. In: Sexual Selection, Testing the Alternatives. Ed. by J. W. Bradbury and M. B. Anderson. New York: John Wiley and Sons. Pp. 83–94.

López-González, C. (1992): Descripción y variación del esqueleto postcraneal de *Glossophaga morenoi morenoi* Martínez y Villa, 1938 (Chiroptera: Phyllostomidae). Unpubl. B.S. Thesis, Escuela Nacional de Ciencias Biológicas, México.

McLellan, L. J. (1984): A morphometric analysis of *Carollia* (Chiroptera, Phyllostomidae). Am. Mus. Novit. **2791**, 1–35.

Mayr, E. (1942): Systematics and the Origin of Species. New York: Columbia Univ. Press.

Myers, P. (1978): Sexual dimorphism in size of vespertilionid bats. Am. Nat. **122**, 701–711.

Polaco, O. J.; Muñiz-Martínez, R: (1987): Los murciélagos de la costa de Michoacán, México. An. Esc. Nac. Cienc. Biól. México **31**, 63–89.

Power, D. M.; Tamsitt, J. R. (1973): Variation in *Phyllostomus discolor* (Chiroptera: Phyllostomidae). Can. J. Zool. **51**, 461–468.

Ralls, K. (1976): Mammals in which females are larger than males. Quart. Rev. Biol. **51**, 245–276.

Rzedowski, J. (1988): Vegetación de México. México: Editorial LIMUSA.

SAS Institute Inc. (1987): SAS, ver. 6.04. SAS Institute Inc., Cary, North Carolina.

Selander, R. K. (1966): Sexual dimorphism and differential niche utilization in birds. Condor **68**, 113–151.

Shine, R. (1989): Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quart. Rev. Biol. **64**, 419–461.

Trivers, R. L. (1972): Parental investment and sexual selection. In: Sexual selection and the descent of man (1871–1971). Ed. by B. Campbell. Chicago: Aldine Atherton Press. Pp. 136–179.

Webster, W. D. (1993): Systematics and evolution of bats of the genus *Glossophaga.* Spec. Pub. Mus., Texas Tech Univ. **36**, 1–184.

Webster, W. D.; Jones, J. K., Jr. (1980): Taxonomic and nomenclatorial notes on bats of the genus *Glossophaga* in North America, with description of a new species. Occas. Papers Mus., Texas Tech Univ. **71**, 1–12.

Williams, D. F.; Findley, J. S. (1979): Sexual size dimorphism in vespertilionid bats. Am. Midl. Nat. **102**, 113–126.

Willig, M. R.; Hollander, R. R. (1995): Secondary sexual dimorphism and phylogenetic constraints in bats: a multivariate approach. J. Mammalogy **76**, 981–992.

Willig, M. R.; Owen, R. D.; Colbert, R. L. (1987): Assessment of morphometric variation in natural populations: the inadequacy of the univariate approach. Syst. Zool. **35**, 195–203.

Authors' addresses: Celia López-González, Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409-3131, USA; Oscar J. Polaco, Subdirección de Laboratorios y Apoyo Académico, Instituto Nacional de Antropología e Historia, Moneda 16, Col. Centro, México, D. F. 06060, México.